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The Mating Behavior of *Papilio glaucus* (Papilionidae)

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Abstract. Male and female *Papilio glaucus* were released in a large flight cage containing vegetation simulating a forest clearing. Observations were made to study courtship behavior and the mating system of *P. glaucus*. Mechanisms of female choice through solicitation of males and rejection behavior during courtship are presented.

Introduction

The tiger swallowtail, *Papilio glaucus* L., has monomorphic non-mimetic males as well as two female forms: one male-like and the other a Batesian mimic of *Battus philenor* L. It has therefore been of interest in studies of assortative mating (Burns, 1966; Platt, Harrison and Williams, 1984) and sexual selection in mimetic species (Brower, 1963; Silberglied, 1984; Krebs, 1986). Despite this general interest, little information is available on its mating behavior. This note describes courtship and mate avoidance behaviors in *P. glaucus* and suggests mechanisms for female choice.

Materials and Methods

Adults were reared from eggs of field-caught females (Virginia) and females sent by Mark Scriber, University of Wisconsin (Wisconsin and Illinois), for experiments in 1984 and 1985. Although geographically variable, all butterflies used were *P. glaucus glaucus*. Larvae were reared on fresh black cherry leaves (*Prunus serotina*) in the laboratory under a long photoperiod to prevent diapause which allowed rearing of three generations.

The experimental population for 1985 was produced by randomly crossing field-caught, Wisconsin, and Illinois butterflies early in the experiment and rearing and crossing these offspring throughout the summer. Observations therefore began with pure strain individuals presented at random and continued with offspring of geographically mixed parentage. Observations made in the Spring of 1984 included only reared Blacksburg individuals.

Observations were made in a flight cage (5 × 8 × 5 m) in Blacksburg, Virginia. The cage resembled a forest clearing with small trees, including *Prunus serotina*, inside. Vines lined the sides and larger trees surrounded the cage.

Because an outdoor cage was used, weather conditions could not be controlled. All observations were made between noon and 4:30 PM on days ranging in temperature from 22 to 33°C. Temperatures outside this range, high winds and cloudy conditions decreased flight too much to allow for efficient testing.

A single virgin female, 1 to 3 days old, was released to one male, 2 to 4 days old.

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Observations were made until either several unsuccessful courtships or a mating occurred. The average observation time was one hour per pair.

Results

General

A total of 196 courtships using 70 *P. glaucus* pairs (17 in 1984 and 53 in 1985) was observed. Of these, 34 (17%) led to matings. Because results were similar when either Virginia butterflies were presented to each other (1984) or the geographically mixed populations (1985) were used, structure of successful courtships versus unsuccessful ones for all presentations are grouped when discussed below.

Successful courtships

Typical courtships leading to copulation involved an exchange of behaviors in flight between males and females. These flights were initiated when responsive males encountered females, usually in air (27 of 34) or on vegetation (6 of 34). Within the cage, males usually initiated courtship. However, in nine courtships leading to copulation, females flew toward the male, soliciting courtship. One such flight was directed to a male on vegetation.

Following initial interactions, females flew up and away from males which pursued 5-15 cm below and behind. Most of these courtship flights therefore occurred along the cage top at 5 m. In two observations butterflies released in the field ascended into and over tree tops and out of sight.

Courtship flights were highly variable in length ($\bar{x}$ = 16.5 s ± 3.9 s, n = 18, range 0-59 s). However, only 7 of 34 matings occurred after the first courtship. Total courtship flight time preceding copulation averaged 58 ± 12 s (n = 18). Successful males averaged 2.6 courtships (n = 34) before they were accepted by females.

Pursuit flights continued until the females landed with wings either open (7 of 31) or closed (24 of 31). The male hovered above the female for a second or two before attempting to land beside her (23 of 34), but sometimes (11 of 34) immediately landed by the female. When a female landed with open wings, the male always hovered. Wing closing by a female was quickly followed by the male alighting beside the female.

Three courtships leading to mating lacked usual courtship flights. In those, the males hovered over the females perched on vegetation, landed and were accepted. However, courtship flights had occurred previously in all three.

A male, once beside the female, extended his abdomen to contact the female's genitalia. After acceptance, he relaxed, dropped below the female and remained stationary in copula for 45 min to an hour. Most matings occurred along the cage top, with only a few as low as three meters. No post copulatory flights were observed unless the pair was disturbed. In flight, females flew with males hanging below.

Unsuccessful courtships

Unsuccessful courtships were ended by either males or females. Of 162 unsuccessful courtships, designated as those interactions between males and females which lasted at least a second, 33 encounters in air never led to a pursuit flight. These interactions ended when males failed to respond to females (26 males, not included in the above total, never courted females presented to them).

Of the other 129 courtship flights, 104 broke up while males were pursuing females. The remaining 25 ended after males interacted with perched females. Because these males were responding positively to females, failure to mate was probably due to behaviors on the part of females to evade or reject courting males.

Unsuccessful courtships lasted longer than those that ended in copulation ($\bar{x}$ = 103 ± 15 s, n = 18, $p<0.02$). Number of courtships, however, did not differ, 2.72 ± .21 for unsuccessful males and 2.56 ± .26 for successful ones ($p>0.3$).

Discussion

Several aspects of *P. glaucus* mating behavior are very different from that of other species. Most notable is the high incidence of courtship solicitation by females. Solicitation flights were generally made directly to males in flight, although perching males were also solicited. Females flew across either from the side or above males within 15 cm, turned, and flew up and away. If males failed to pursue, solicitation was often repeated.

Solicitation flights have also been observed in *Pieris protodice* Boisduval and LeConte (Rutowski, 1980), *Heliconius erato* L. (Crane, 1955), *Danaus gilippus* Cramer (Brower, Brower and Cranston, 1965) and *Aphantopus hyperanthus* L. (Wicklund, 1982). In *P. glaucus*, solicitations were observed for 53% of males that mated; 9 of 34 matings had been immediately preceded by solicitation. Thirty-seven percent of all first interactions between males and females were initiated by females. Also, of 26 males that were not responsive to females, 85% received solicitations.

A second unusual feature of *P. glaucus* courtship is lack of antennal contact between males and females. Brower et al. (1965) described males of *D. gilippus* brushing antennae of females with specialized scent scales. Scent is important in courtship to many other butterfly species (Thornhill and Alcock, 1983). However, as *P. glaucus* males court from below and behind females, some wing contact occurs from below but none near the female's head. Opportunity to pass scent did occur when females landed but only occasional wing contact was observed before the male attempted to land and copulate. These behaviors suggest that visual cues are far more important than olfactory in mate choice in this species.

With only 17% of all courtships with virgin females leading to matings, females are able to reject and avoid males. Longer courtship times of unsuccessful males suggested that females avoided landing until pursuing males were evaded.

Two observed avoidance postures were closing and depressing the wings when a male flew near, and depressing the abdomen to the substrate to avoid genital contact when a male landed. Rejection behaviors during pursuit included "quick landing," a sudden stop with wings closed and depressed, and "dropping," a relaxed free fall into brush. Females also employed slow descending flights, which forced males to abandon courtship when females hovered less than 30 cm above the ground. Two less obvious behaviors were flying through thick brush, also observed in *D. gilippus* (Brower et al. 1965), and simply not flying, a behavior I observed when females were released with a high male density. Virgin females have been observed to reject males by like means in other species (Rutowski, 1982, 1984).

Comparisons in this study suggested no differences between male responses to the two female forms, mimetic and male-like. While the experimental design did not provide for controlled comparisons of details within courtship flights, overall mating success and male courtship frequency were not different.

One question in this study is its application to mating behavior in nature. Only two courtship flights, described earlier, were observed outside of the cage, although releases, albeit unsuccessful, were attempted. However, vegetation within the cage, and its size, provided more natural conditions than in most other cage studies.

Brower (1963) says that *P. glaucus* males fly around courting any females located. No other description of a mating system exists for this species, and no territorial behavior is known. Multiple male releases in the cage elicited no male-male interaction. Attempts by several males to court the same female simultaneously were observed. None were successful. Only in mudpuddling aggregations are high densities of males found.

Rutowski (1984) suggests that prolonged searching polygyny is the most likely mating system to be found in butterflies. Strong rapid flight, lack of male-male competition and dispersed abundant food and oviposition sites suggests the existence of this system in *P. glaucus*.

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